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Plant and bird diversity in rubber agroforests in the lowlands of Sumatra, Indonesia

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Abstract Plant and bird diversity in the Indonesian jungle rubber agroforestry system was compared to that in primary forest and rubber plantations by integrating new and existing data from a lowland rain forest area in Sumatra. Jungle rubber gardens are low-input rubber (*Hevea brasiliensis*) agroforests that structurally resemble secondary forest and in which wild species are tolerated by the farmer. As primary forests have almost completely disappeared from the lowlands of the Sumatra peneplain, our aim was to assess the contribution of jungle rubber as a land use type to the conservation of plant and bird species, especially those that are associated with the forest interior of primary and old secondary forest. Species-accumulation curves were compiled for terrestrial and epiphytic pteridophytes, trees and birds, and for subsets of 'forest species' of terrestrial pteridophytes and birds. Comparing jungle rubber and primary forest, groups differed in relative species richness patterns. Species richness in jungle rubber was slightly higher (terrestrial pteridophytes), similar (birds) or lower (epiphytic pteridophytes, trees, vascular plants as a whole) than in primary forest. For subsets of 'forest species' of terrestrial pteridophytes and birds, species richness in jungle rubber was lower than in primary forest. For all groups, species richness in jungle rubber was generally higher than in rubber plantations. Although species conservation in jungle rubber is limited by management practices and by a slash-and-burn cycle for replanting of about 40 years, this forest-like land use does support species diversity in an impoverished landscape increasingly dominated by monoculture plantations.

Keywords Biodiversity · Conservation · Jungle rubber · Rubber plantation · Species-accumulation curves · Tropical rain forest

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Introduction

Rubber agroforest as a disturbed forest type

In areas undergoing rapid land use change such as the lowlands of Sumatra, where undisturbed lowland forest has almost completely disappeared (Lambert and Collar 2002), the question whether at least some of the lowland rainforest species can survive in disturbed forest types has become important. The potential significance of agricultural production systems for biodiversity conservation is stressed by nature conservation agencies and the international research community (WRI 1992, pp. 110–115, 128, and 130; Halladay and Gilmour 1995; Collins and Qualset 1999; Siebert 2002; García-Fernández et al. 2003; Garrity 2004; Schroth 2004).

Most primary forests and logged forests in the lowlands of Sumatra have been converted since the 1970s to large scale monoculture plantations (oil palm, rubber, industrial timber) as well as transmigration sites (World Bank 2001). Smallholder rubber agroforest, also called 'jungle rubber' (Gouyon et al. 1993), on the other hand is a major land use type in the Sumatran lowlands that has existed since the beginning of the 20th century. With current land use changes, it may become the most extensive forest-like vegetation type in the area.

Even though these agroforests are planted and owned by a farmer, the component of spontaneous secondary vegetation in these agroforests is large enough to regard them as a type of disturbed or secondary forest vegetation in the context of biodiversity research. Jungle rubber gardens are usually weeded for the first 2–3 years after slash-and-burn, when rice and vegetables are grown together with newly planted rubber tree seedlings. No herbicides or fertilisers are used. After the first few years, most wild species that colonise the gardens are allowed to grow with the rubber trees, and a complex forest-like vegetation develops. In mature gardens, management is usually limited to maintaining paths between rubber trees to allow for tapping. Jungle rubber gardens are on average replanted after about 40 years, but some gardens are maintained to an age of 70–80 years. Gouyon et al. (1993) found that two older jungle rubber gardens (35–40 years old and 40–45 years old) were structurally similar to secondary forest. Older jungle rubber gardens (>30 years old) can reach a height of 20–40 m in the Jambi lowlands, compared to 43–60 m for primary forests in the same area (H. Beukema, unpublished data). The percentage of trees that are rubber trees is variable, and declines with the age of the garden. On average, about 40 - 50 % of the trees in mature gardens are rubber trees (Hardiwinoto et al. 1999).

As a land use type, jungle rubber will most probably remain important. Smallholder rubber covered about 530,000 ha in Jambi province in 1996 (Dinas Perkebunan Jambi 1998, p. 27) and almost three million hectares in Indonesia in 1997 (Ministry of Forestry and Estate Crops 1998). Economic prospects for rubber on the world market are positive (Smit and Vogelvang 1997; Burger and Smit 1998, 2000) and production by smallholders is still profitable (Levang et al. 1999; Suyanto et al. 2001).

Michon and De Foresta (1992) drew attention to the issue of complex agroforestry systems and conservation of biological diversity in Indonesia. They pleaded for ''assessment of existing and potential capacity of agricultural ecosystems to preserve biological diversity'' and presented inventory data on vegetation of multistrata agroforestry systems in Sumatra. Their early conclusion was that agroforests cannot replace protected forest reserves but can ''contribute to maintaining in the landscape a useful and diversified forest ecosystem from which the peasant is not excluded''. However, they also remarked at the time that ''reliable comparisons of biodiversity levels between forest and agroforestry ecosystems have still to be done''. In this paper we summarise such comparisons, combining plant and bird data from published papers, research reports, and our own research in Sumatra.

The aims of this study are:

- To compare diversity patterns of plants and birds, as well as subgroups of plants such as pteridophytes and trees, in three land use types: primary forest, jungle rubber, and rubber plantations, in the lowlands of Sumatra.

- To assess the contribution of jungle rubber as a land use type to the conservation of plant and bird species that are associated with the forest interior of primary and old secondary forest.

Sampling for biodiversity research in jungle rubber

Sampling in jungle rubber is complicated by the internal variability of this land use type. It is a cultivation system of smallholder farmers who usually own several small and scattered rubber gardens of different ages and varying in size from less than one to a few hectares. This results in a rubber landscape that is a mosaic of small gardens of different ages, rubber densities and management intensities. Because slash-and-burn is used to establish rubber gardens, 'wild' species have to establish themselves anew by invasion from surrounding areas, or regenerate from the seedbank or sprouting stumps. Succession starts from burned and weeded fields and is influenced by source populations in surrounding areas, by selective activities of farmers and by the cultivation history of the garden. The resulting variety within the jungle rubber land use type cannot be fully captured by data collected in a single or a few gardens. Sampling a larger set of gardens or a transect that more or less represents the land use type as a whole is required to study biodiversity in jungle rubber.

Scale-dependency of effects of disturbance is another complicating factor for biodiversity research in jungle rubber. Scale effects are important in disturbance studies (Hill and Hamer 2004). Hamer and Hill (2000) investigated the effect of the spatial scale at which Lepidoptera communities were sampled, and found that "disturbance had opposite effects on diversity at large and small scales: as scale decreased, the probability of a positive effect of disturbance on diversity increased".

To account for the internal variability of the land use type and the scale-dependency of effects of disturbance, datasets should ideally be large and cover a large number of jungle rubber gardens. However, a practical problem that arises when sampling diverse groups in a range of gardens is the large number of specimen to be identified. For vascular plants, sampling of a single 0.02 ha plot in a jungle rubber garden already yielded more than 100 species (Gillison et al. 1999). The largest available dataset comparing forest and jungle rubber for vascular plants contains hundreds of species, for which more than 1000 herbarium specimen were analysed (Michon and De Foresta 1995), while its data for jungle rubber was collected in two gardens only.

Limiting sampling to particular subgroups, such as ferns or trees, allows for collection of data over a larger number of gardens. However, species richness patterns found for such subgroups may differ and the issue of representativeness needs to be addressed. For instance, we may assume that for the group of vascular plants as a whole, the general trend is most likely a decrease in species richness with disturbance from forest to jungle rubber to rubber plantation. However, different components or subgroups within the group of vascular plants would not necessarily have to conform to this trend. Speed of (re)colonisation and suitability of the rubber habitat will differ for different subgroups of plants.

Conservation of forest species in jungle rubber

Plant and bird species that are associated with the forest interior of primary and old secondary forest are most affected by habitat loss through large scale forest conversion in the Sumatran lowlands. To assess the contribution of jungle rubber to the conservation of those species that are most in need of protection, we need to look not just at total plant or bird species diversity in jungle rubber, but also at the relation of different groups of species to disturbed forest habitat and forest succession. The invasion of non-forest species or early-successional species may obscure our view on the reduction of true forest species with disturbance. For instance, species of terrestrial pteridophytes vary in their requirements for shade, and groups of 'forest species' and 'non-forest species' of terrestrial pteridophytes can be distinguished based on those requirements (Beukema and Van Noordwijk 2004). Epiphytes on the other hand are mostly related to old secondary forest and primary forest, as they depend on the development of tree trunks and branches for their habitat. Habitat requirements of birds have been studied well enough to allow for basic grouping of species by their main natural habitat in the Sumatran lowlands and their level of association with lowland forest.

Rapid assessment studies (Gillison 2000) have indicated that jungle rubber and other moderately disturbed types such as logged forest and old secondary forest 'score' rather high on total species richness. It is especially important to interpret those results in terms of ecological groups, and to investigate whether high species richness values found for jungle rubber could be due to invasion of non-forest species or to scale effects.

Methods

Study area

All data presented are from lowland areas (<150 m above sea level) in Sumatra. Most research was done in Jambi province and, across the northern provincial border of Jambi, in Riau province (Fig. 1).

Annual rainfall in the Jambi peneplain is about 3,000 mm per year. On average, there are 7–8 wet months (>200 mm rainfall/month) per year, and no months with less than 100 mm of rainfall. The driest months are from May to September. Yearly average minimum and maximum temperatures are 22.5°C and 31.4°C, respectively. The terrain is slightly undulating to flat, and soils are predominantly well-drained, acid oxisols with low fertility. Biophysical, socio-economical and historical aspects of land use, including jungle rubber, in central Sumatra are described in Gouyon et al. (1993), Potter and Lee (1998), Sandbukt and Wiriadinata (1994), Tomich et al. (1998), and Van Noordwijk et al. (1995). The 'forest' land use type in the datasets in this paper (indicated as 'forest' or 'primary forest') comprises old growth mixed Dipterocarp lowland rain forest (Laumonier 1997) without visible traces of timber cutting and without known history of logging or shifting cultivation, the only human use being limited collection of non-timber forest products and hunting.

Large areas of (mostly logged) forest still present in Jambi Province during the sampling period (1990–1999) were located in the foothills of the Barisan Range to the west, bordering the Kerinci Seblat National Park, and in a belt of forest near the border with Riau Province to the north, including the Bukit Tigapuluh Range (see also the maps in Potter and Lee 1998). In the more agricultural central and southern parts of the province, a few small fragments of primary forest as well as some larger fragments of logged forest remained at the time. Except for the small Pasir Mayang study area to the north, most primary forests in this study have since been logged or converted to other uses. Very little unlogged forest now remains in the area, and conversion of logged forest is still ongoing. A recent land use change study (Ekadinata et al. 2004, Ekadinata et al. unpublished data) based on remote sensing images of Bungo district, in the western part of Jambi province, indicates a change in forest cover from 70% of the total area in 1973 to 51% in 1988 and 28% in 2002, with remaining forest cover mostly located at higher altitudes in the Barisan Range. Jungle rubber cover was 16% in 1973 and 17% in 1988, and down to 13% of the total area in 2002, while monoculture plantations (rubber and oilpalm) increased steadily, covering 6% in 1973, 23% in 1988, and 46% of Bungo district in 2002. About 16% of our sampling locations were located in Bungo district, which comprises a 4550 km^2 area or about 9.2% of Jambi Province.

Datasets

All vascular plants

Two datasets were available for comparison of species richness of vascular plants in forest, jungle rubber and rubber plantations in Sumatra: one by De Foresta (unpublished corrections of data in De Foresta 1991 and Michon and De Foresta 1995) and one by Gillison et al. (1999). De Foresta sampled vascular plant species along 100 m line transects. One transect was sampled in forest

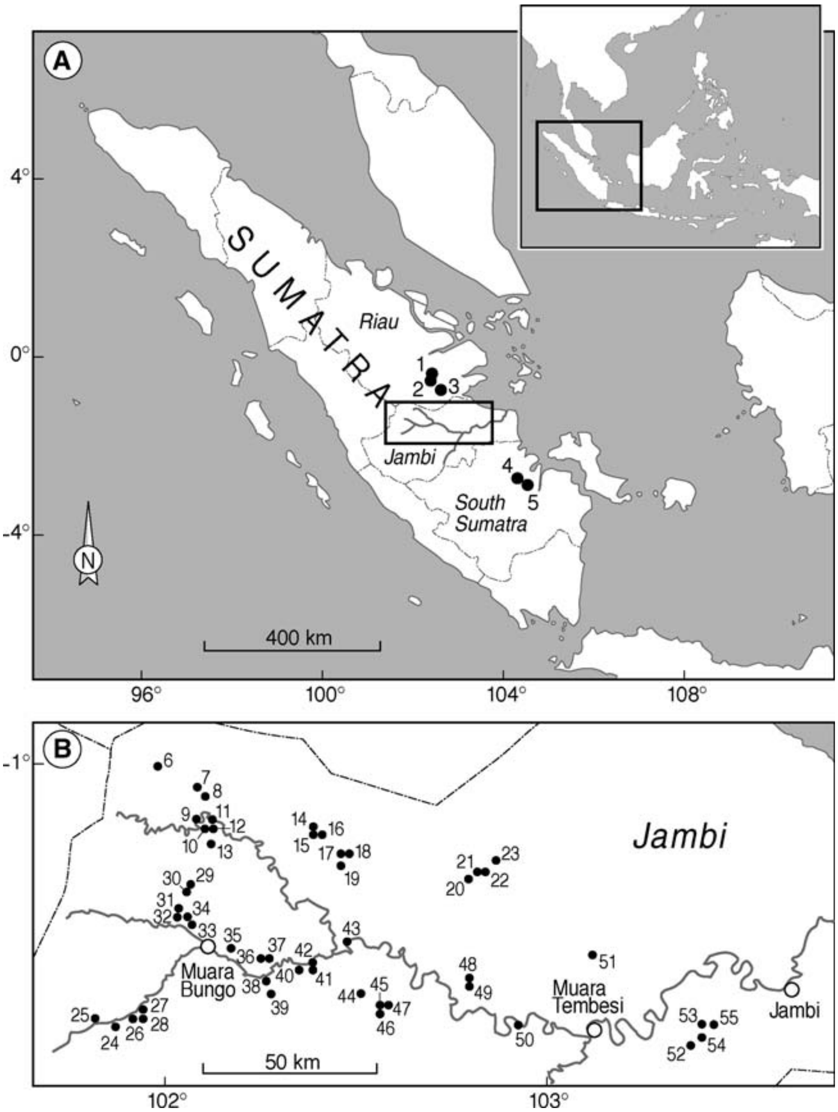

Fig. 1 Research areas in the lowlands of Sumatra, Indonesia, in the provinces of Riau and South Sumatra (**A**) and Jambi (**B**). Riau: Sibabat Dua (1), Pangkalan Kasai (2), Talang Lakat/Sungai Akar (3); South Sumatra: Sukaraja (4), Sembawa Research Station (5). Jambi: Pasir Mayang (6–8), Teluk Cempako (9), Pancuran Gading (10), Dusun Tuo Ulu (11–13), Semambu (14–16), Muara Sekalo (17–19), Lubuk Kambing (20–23), Muara Buat (24), Rantau Pandan (25–28), Wiroto Agung (29, 30), Rimbo Bujang (31–33), Sarana Jaya (34), Babeko (35), Sepunggur (36, 37), Muara Kuamang (38, 39), Sungai Bungur (40), Sungai Tilan (41, 42), Semabu (43), Silva Gama (44), Pintas Tuo (45–47), Bukit Sari (48, 49), Sungai Puar (50), Rantaupuri (51), Batin (52), Muara Bulian (53, 54), Maro Sebo (55). Sampling by different researchers in forest (f), jungle rubber (j) and rubber plantation (p). Vascular plants: De Foresta 5p, 24j, 26f, 28j, Gillison et al. 7f, 8p, 10j. Pteridophytes: Beukema 7f, 8p, 9j, 11p, 12p, 13p, 14j, 15j, 16f, 17f, 18f, 19j, 20f, 21j, 22p, 23j, 29p, 30p, 31p, 32p, 33p, 34p, 35p, 35j, 39j, 40j, 41j, 42j, 43p, 44f, 48f, 49f, 50j, 52p, 53p, 54p, 55p. Trees: Laumonier 7f, Franken and Roos 6f, 51f, Vincent et al. 39j, Hardiwinoto et al. 24j, 27j, 28j, 36j, 37j, 38j, 39j, 45j, 46j, 47j, De Foresta 4j, Kheowvongsri 24j. Birds: Danielsen and Heegaard 1p, 2j, 3f, Jepson and Djarwadi 7f, 8p, 10j, Thiollay 25j

and two transects in jungle rubber, in two different gardens, both 50–60 years old, in 1993. Mean size of jungle rubber gardens in the area (Muara Buat in Jambi) was about 1 ha (H. de Foresta, pers. comm.). One transect was sampled in a 20-year-old rubber plantation in 1991.

Gillison et al. sampled vascular plant species in 40 m × 5 m (0.02 ha) plots. Two replicate plots per land use type were sampled in a patch of forest, a jungle rubber garden (age uncertain), and a 16-year-old rubber plantation, in 1997. All data were from Jambi province except for the rubber plantation transect by De Foresta, which was in South Sumatra province.

Pteridophytes

Terrestrial and epiphytic pteridophyte species were sampled in 40 m × 40 m (0.16 ha) plots in primary forest, jungle rubber gardens and rubber plantations throughout the peneplain of Jambi province, Sumatra (Beukema and Van Noordwijk 2004; H. Beukema, unpublished data). Total sampled area for terrestrial pteridophytes was 1.76 ha in 11 primary forest plots, 3.68 ha in 23 jungle rubber plots (in 23 different gardens) and 2.72 ha in 17 rubber plantation plots (in 17 different plantations). Epiphytic pteridophytes were sampled in the same plots except for one primary forest plot that was not sampled for epiphytic pteridophytes. The epiphytic species *Asplenium nidus L.* and *A. phyllitidis Don* were analysed as one species because of difficulty of identification. Age ranges of the rubber plots were characteristic of the productive phase of the respective land use types: 9–74 years old for jungle rubber plots, and 5–19 years old for rubber plantation plots. Of the jungle rubber plots, 57% were in older gardens (>30 years old). The size of sampled primary forest fragments ranged from a few ha to 900 ha. Mean garden size of sampled jungle rubber gardens was 2.2 ha. Of the 17 rubber plantation plots, 11 were in smallholder plantations with an average size of 2.4 ha, while 6 plots were in large plantations covering tens to hundreds of hectares. Sampling took place in 1996, 1997 and 1998.

Subgroups of vascular plants

In the pteridophyte plots described above, presence/absence of palms (including rattans), lianas, and epiphytic orchids was noted. A subgroup was present in a plot when at least one individual of any size belonging to that subgroup was found in the plot, regardless of species.

Trees

An overview of datasets on trees collected by different researchers in either forest or jungle rubber is given in Table 1.

For trees, we found no single dataset from Sumatra that included both forest and jungle rubber samples. However, several datasets collected by different researchers in either forest or jungle rubber could be compared as they all distinguished individuals at the species level, used area-based plots and measured tree size as Diameter at Breast Height (DBH). Trees with a

Table 1 Tree datasets

Author	Sampling unit	Land use type	Number of sampling units (plots or subplots)	Sampled area
Laumonier	0.04 ha subplots	Primary forest	150 contiguous subplots	6 ha
Franken and Roos	0.2 ha plots	Primary forest	3 plots, different locations	0.6 ha
Vincent et al.	0.04 ha subplots	Jungle rubber	25 contiguous subplots in one garden	1 ha
Hardiwinoto et al.	0.2 ha plots	Jungle rubber	16 plots in 16 different gardens in 4 villages	3.2 ha
De Foresta	0.1 ha plot	Jungle rubber	1 plot (in 1 garden)	0.1 ha
Kheowvongsri	Various plot sizes	Jungle rubber	4 plots in different gardens (0.05 + 0.07 + 0.12 + 0.13 ha)	0.37 ha

Type and size of sampling unit, sample size, and total area sampled for tree diversity data of several authors. Data from Jambi province, except for De Foresta's jungle rubber plot in South Sumatra. The plot by Vincent (permanent sampling plot, G. Vincent et al. unpublished data, ICRAF 2001) is in one of the gardens sampled by Hardiwinoto minimum size of 10 cm DBH were selected from the datasets in Table 1 to be included in our analysis. Laumonier (1997) collected the data used in this study in 1991–1992. Franken and Roos (1981) sampled in 1981. The jungle rubber plot by Vincent et al. (unpublished data, ICRAF 2001) was 34 years old when sampled in 1999. Ages of the 16 jungle rubber gardens sampled in 1998–1999 by Hardiwinoto (1999) are unknown. The jungle rubber plot by De Foresta (1991) was about 35 years old when sampled in 1991, while the four plots by Kheowvongsri (1990) were 10, 15, 15, and over 20 years old when sampled in 1990.

Birds

We used bird studies over a range of land uses by Danielsen and Heegaard (1995, 2000) and Thiollay (1995), and a rapid assessment by Jepson and Djarwadi (1999), see Table 2.

Danielsen and Heegaard used a variable distance line-transect method (Buckland et al. 1993), while Jepson and Djarwadi collected their data by roaming around a plot centre during three hours by two persons. Thiollay did not sample for a fixed period of time, but finished a sample when 50 individuals were recorded. A list of observations from all three datasets is presented in Appendix 2. Further details on the field methods are provided in Danielsen and Heegaard (1995, 2000), Jepson and Djarwadi (1999), and Thiollay (1995).

How many gardens were covered by the jungle rubber transect of Danielsen and Heegaard (1995, 2000) is unknown, but since the average size of jungle rubber gardens in their study area was 1.2 ha (A. Angelsen, pers. comm.), their 2,000 m transect must have crossed a number of gardens. Although ages of those gardens are unknown, data on tree height and composition suggest that some older gardens were included in their study. Of 81 trees (>10 cm DBH) measured along their jungle rubber transect, 36% were rubber trees ranging in height from 9 m to 23 m, while the other trees ranged in height from 6 m to 26 m (Danielsen and Heegaard, unpublished data). The jungle rubber garden (age uncertain) and the rubber plantation (16 years old) sampled by Jepson and Djarwadi (1999) were the same as those sampled by Gillison et al. (1999) for vascular plants. The 28 jungle rubber transects in the study by Thiollay must have included many different gardens, but ages are unknown. Thiollay (1995) mentions a range of 30–80% rubber trees, and canopy height of 20–30 m, which suggests that some older gardens were included. Sampling by Danielsen and Heegaard took place in 1991, by Jepson and Djarwadi in 1997 and by Thiollay in 1991 and 1992.

Aerial insectivorous birds were not included in the study as they are almost impossible to detect in closed-canopy forest. Unidentified birds and birds identified to family or genus level but not to species level were excluded from our analyses. Excluded individuals comprised 14.5% of total

Table 2 Bird datasets

Author and sampling method	Land use type	Sampling effort	Recorded bird individuals
Danielsen & Heegaard; observers moving along a 2,000 m line transect	Primary forest	1 transect; 40 man-hours	1,291
	Jungle rubber	1 transect through several gardens; 40 man-hours	1,281
	Rubber plantation	1 transect through 1 plantation; 20 man-hours	3,014
Jepson & Djarwadi; observers moving within 30 m of a plot centre	Primary forest	2 plots in 1 forest; 12 man-hours total	Not recorded
	Jungle rubber	1 plot (in 1 garden); 6 man-hours	Not recorded
	Rubber plantation	1 plot (in 1 plantation); 6 man-hours	Not recorded
Thiollay; 50 individuals per transect	Jungle rubber	28 transects, >300 m apart, in different gardens in 20 km radius	1,388

Sampling method, sampling effort, and number of bird individuals recorded for bird diversity data of several authors. Data from Jambi (Jepson and Djarwadi, Thiollay) and Riau (Danielsen and Heegaard) bird individuals recorded by Danielsen and Heegaard (1995, 2000) and 2.6% of bird individuals recorded in jungle rubber by Thiollay (1995). From the dataset of Jepson and Djarwadi (1999) 10 unidentified species were excluded, all in primary forest.

Species-accumulation curves

To account for effects of scale and sample size, we summarised data where possible as species-accumulation curves. Species-accumulation curves were compiled for terrestrial pteridophytes, epiphytic pteridophytes, trees, and birds in several land use types. For trees, land use types included primary forest and jungle rubber, while for pteridophytes and birds also rubber plantations were included. Curves were generated for each source dataset separately.

To remove the effect of plot order in the accumulation curves, the program EstimateS (Colwell 1997) was used to randomise plot sequence in each sample and derive average values for the cumulative number of species at each number of sampling units. Those derived values for the cumulative number of species were then plotted against the natural logarithm of area (in hectares) or time (in man-hours). Where data for different land use types were collected in a comparable manner, regression lines were drawn through the datapoints for those land use types to facilitate visual comparison. The ranges of area or time over which such linear relationships are shown were determined by the land use type with the smallest number of sampling units. The linear relationships were in fact linear parts of sigmoid relationships, but datasets were not sufficiently large in all cases to show sigmoid relations.

For trees, data from two small datasets (De Foresta 1991, 0.1 ha, and Kheowvongsri 1990, 0.37 ha) were added as single data points to the figure containing the species-accumulation curves.

In addition to the species-accumulation curves for trees that were based on sampled area, we constructed species-accumulation curves for trees based on recorded individuals using the largest datasets collected in primary forest (Laumonier 1997) and in jungle rubber (Hardiwinoto et al. 1999). We removed the rubber trees from the jungle rubber data to show diversity of non-rubber trees in jungle rubber gardens as compared to tree diversity in primary forest. Note that the datasets in this comparison were not collected by the same method (contiguous subplots in primary forest versus non-contiguous plots in jungle rubber).

For birds, we compared the datapoints of the smaller dataset of Jepson and Djarwadi (1999) to datapoints belonging to the species-accumulation curves based on the larger dataset of Danielsen and Heegaard (1995, 2000). These two datasets could be compared because sampling effort was quantified by the same measure (man-hours). Species-accumulation curves for terrestrial pteridophytes were published earlier (Beukema and Van Noordwijk 2004).

Species grouping

Individual species of terrestrial pteridophytes and birds were grouped according to their ecological requirements and preferred habitats. Species accumulation curves were subsequently constructed for the subsets of species that were mainly associated with primary and late secondary forest (‘forest species’).

Terrestrial pteridophytes

Beukema and Van Noordwijk (2004) grouped terrestrial pteridophytes ecologically according to preferred light conditions and habitat as documented in the literature. Species classified as ‘forest species’ were all species that require shade or deep shade plus species that prefer light shade and grow in forest. Classified as ‘non-forest species’ were all species of open and open/light shade conditions plus species that prefer light shade and habitats other than forest (roadsides, forest edges, plantations etc.). For a list of species names and their classification see Beukema and Van Noordwijk (2004).

Birds

Bird species were grouped by preferred habitat (see Appendix 2) using data in Van Marle and

Voous (1988) and MacKinnon and Phillipps (1993), supplemented with Winkler et al. (1995) and personal observations by Danielsen and Heegaard in Sumatra. We classified bird species broadly into three categories (modified from Thiollay 1995) according to their main natural habitat in lowlands and their level of association with lowland forest, as follows:

Habitat group 1 = Species mostly associated with the primary and old secondary forest interior. Some of them are restricted to large, undisturbed forest tracts, but others are more tolerant of human or natural disturbance and remain widespread in more secondary forests.

Habitat group 2 = Species mostly found along edges, in gaps (tree falls, landslides), or in the upper canopy of dense forest stands or in semi-deciduous, more open forest types. They readily occupy degraded secondary forests, tree plantations, and clearings.

Habitat group 3 = Species of open woodlands, low secondary growth, grasslands, inhabited and cultivated areas.

To analyse changes in bird species composition with disturbance, we compared the relative importance of habitat groups in the three land use types. This was done by calculating, for each dataset, the relative number of species of each habitat group in each land use type expressed as a percentage of the total number of species recorded for that land use type.

Relative species richness

To summarise our data on species diversity in jungle rubber as compared to that in primary forest, and to compare subgroups with each other for the effect of disturbance on their relative species richness, we expressed for each subgroup the species richness in jungle rubber as a percentage of the species richness in undisturbed forest, by sampled area for plant groups and by sampling time for birds. Percentages for terrestrial and epiphytic pteridophytes, trees, and birds were based on the average cumulative richness values derived after randomising plot sequence in EstimateS. For trees, percentages were calculated by comparing datasets that were collected in the same way (either contiguous subplots or plots from different locations in Jambi province).

Results

Results by group

All vascular plants

The datasets by Gillison et al. and by De Foresta (see Table 1) consisted of a few small plots or transect lines, for which results are displayed in the form of datapoints (Fig. 2).

Both the line transect data and the combined plot data show a decline in species richness with disturbance. Differences in species richness between land use types were larger for the line transect dataset of De Foresta.

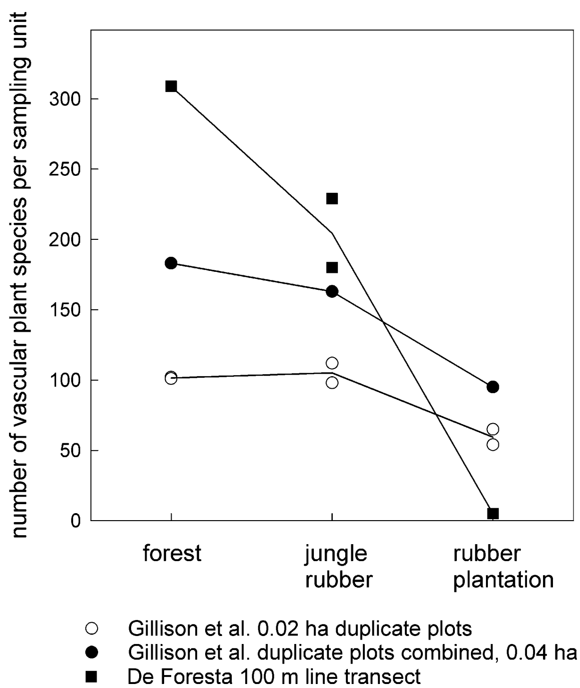

Fig. 2 Number of species of vascular plants per 100 m line transect (De Foresta) or plot (Gillison et al.) in three land use types. De Foresta sampled two different jungle rubber gardens. Gillison et al. sampled two 0.02 ha replicate plots per land use type. Replicate plots were located in the same patch of forest, jungle rubber garden or rubber plantation. Datapoints are shown for replicate plots separately (2 points per land use type) and for the combined replicates (one point per land use type representing 0.04 ha)

Subgroups of vascular plants

Based on the pteridophyte plots of Beukema, Fig. 3 shows the percentage of plots in each land use type in which a subgroup was present.

Figure 3 shows differences in recolonisation of jungle rubber and rubber plantations by different subgroups of vascular plants. Terrestrial pteridophytes were present in all plots, and we observed that they grew more abundantly in rubber plots than in forest. On the other hand, epiphytic orchids recolonised to a lesser extent than the other subgroups. They were absent from half of the jungle rubber plots and were not found in any of the rubber plantation plots. We observed that epiphytic orchids, when found in jungle rubber, were often represented by only a few immature plants and were always much less abundant than epiphytic pteridophytes. In forest, both epiphytic pteridophytes and epiphytic orchids were abundant and often formed large clumps.

With respect to the rubber land use types, Fig. 3 shows that for all subgroups except terrestrial pteridophytes, presence of subgroups of vascular plants was higher in jungle rubber than in rubber plantations. Palms (including rattans) were found in a single rubber plantation only, while lianas were not found in rubber plantations.

Epiphytic pteridophytes

Species-accumulation curves for epiphytic pteridophytes are shown in Fig. 4.

Figure 4 shows that richness in epiphytic pteridophyte species was lower in jungle rubber than in forest, and somewhat lower again in rubber plantations. The datapoints for rubber plantations were all below those for jungle rubber, and the trend in the data indicates that it is improbable that the curves of jungle rubber and rubber plantations would cross when a larger area would be sampled. However, more samples would be needed to determine whether diversity of epiphytic pteridophytes in rubber plantations is actually similar or slightly lower than in jungle rubber.

A list of scientific names of epiphytic pteridophyte species by land use type is given in Appendix 1. With regard to species composition, we noted that most species found in jungle rubber (78%) and rubber plantations (75%) were also found in forest plots. Although these percentages are of course scale-dependent, they serve to indicate that for epiphytic pteridophytes there was apparently not a large shift in species

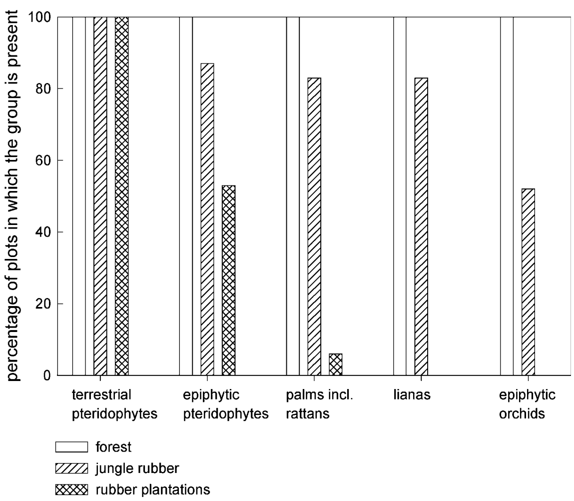

Fig. 3 Percentage of plots in which a subgroup of vascular plants is represented by at least one individual (11 forest plots, 23 jungle rubber plots and 17 rubber plantation plots of 40 m × 40 m). Lianas and epiphytic orchids are absent from all rubber plantation plots

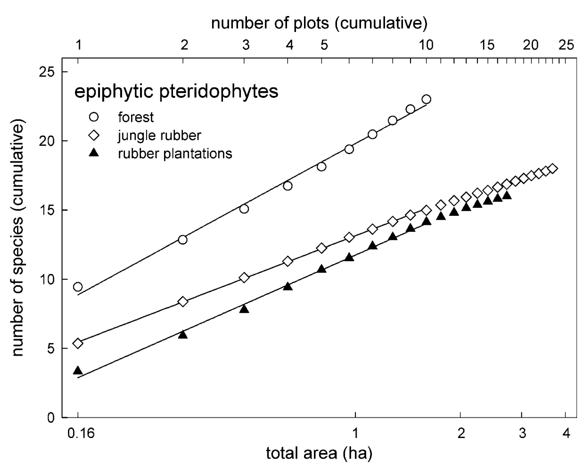

Fig. 4 Species-accumulation curves for epiphytic pteridophytes in 40 m × 40 m plots in forest (10 plots), jungle rubber (23 plots) and rubber plantations (17 plots) in Jambi province, Sumatra. Data by H. Beukema

composition. There was a substantial drop in number of species with disturbance however, and 33% of the species found in primary forest plots were never seen in jungle rubber or rubber plantations in the area.

Trees

Species-accumulation curves and individual datapoints from the datasets presented in Table 1 are plotted by area in Fig. 5.

Figure 5 shows that tree species richness in jungle rubber gardens was relatively low as compared to primary forest. The figure also shows that tree species richness values for jungle rubber, as collected by different researchers, were in close agreement when all results were arranged by sampled area. Of the two forest datasets, richness values found by Franken and Roos (1981) were slightly lower than values found by Laumonier (1997), because one of their three plots was dominated by ironwood (*Eusideroxylon zwageri*) and less rich in other tree species.

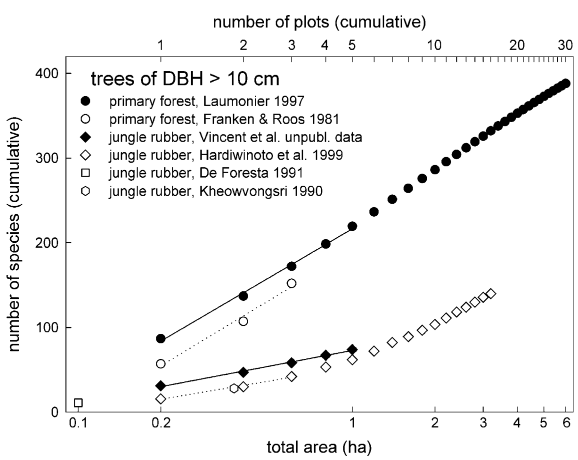

Fig. 5 Species-accumulation curves and datapoints for trees of DBH over 10 cm, Jambi province, Sumatra. Data by several authors. The plots are contiguous for the dataset by Laumonier (1997, Pasir Mayang) and for the subplots of the 1 ha jungle rubber permanent plot of Vincent (G. Vincent, unpublished data), all other plots are non-contiguous. Regression lines are added for datasets that were collected by the same method: solid lines for contiguous subplots (1 ha), dotted lines for non-contiguous plots (0.6 ha). Four small plots by Kheowvongsri (1990) were lumped together to produce one datapoint. The 0.1 ha plot by De Foresta (1991) is from South Sumatra. For further information about the datasets see the original publications

Trees excluding rubber

Tree species richness on a per-area basis in rubber agroforests is lowered by the dominance of *Hevea brasiliensis* itself, which is an exotic tree species from South America. With respect to tree species richness, rubber agroforests may probably be regarded as a 'diluted' secondary forest. To have an impression of the size of this 'dilution effect', we have plotted tree species richness of two datasets from Fig. 5 (Laumonier 1997 for primary forest, Hardiwinoto et al. 1999 for rubber agroforests) against the number of individuals sampled, with and without rubber trees (Fig. 6). It should be noted that data from the two land use types were not collected by the same method: the primary forest data consisted of contiguous subplots in one large forest plot, whereas the rubber agroforest plots were each in a different garden, in several locations.

However large the difference between the data for jungle rubber with and without rubber trees, tree species diversity on a per individual basis was still much higher in primary forest than in jungle rubber. Figure 6 also shows a difference between

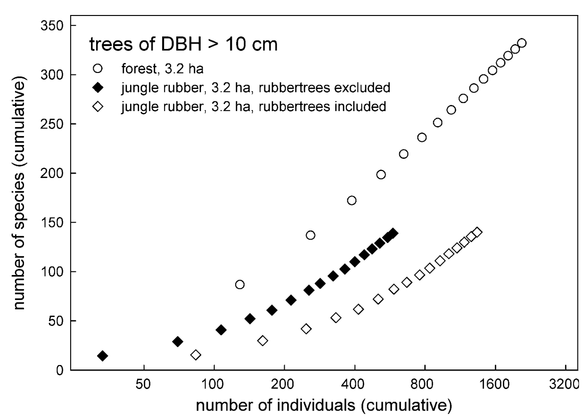

Fig. 6 Species-accumulation curves for individual trees of DBH over 10 cm, for 3.2 ha of primary forest (Laumonier 1997, dots) and 3.2 ha of jungle rubber (Hardiwinoto et al. 1999, diamonds). Open diamonds: all trees including rubber trees. Filled diamonds: rubbertrees excluded from the jungle rubber data

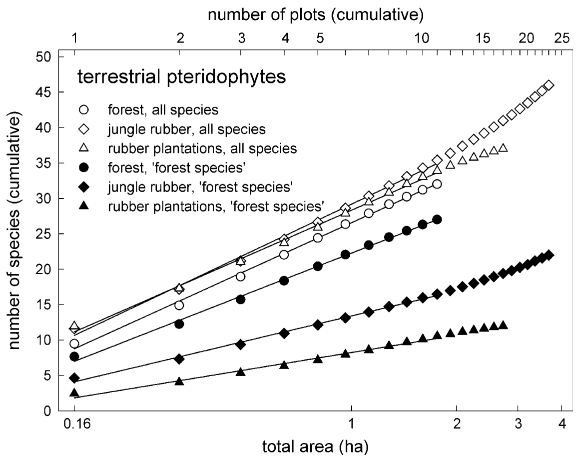

Fig. 7 Species-accumulation curves for terrestrial pteridophytes in forest (dots), jungle rubber (diamonds) and rubber plantations (triangles). Open symbols: all terrestrial pteridophyte species; filled symbols: 'forest species' subset. Plots were 0.16 ha each, non-adjacent and spread over a large area in Jambi province (see Fig. 1)

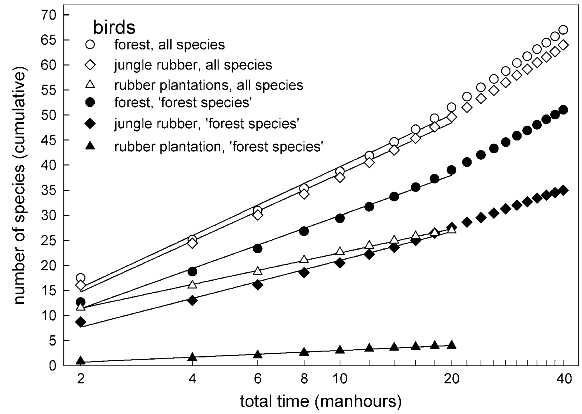

Fig. 8 Species-accumulation curves for the bird data of Danielsen & Heegaard. Open symbols: all birds identified to species level. Filled symbols: subset of 'forest species' classified in habitat group 1: species mostly associated with the primary and old secondary forest interior

forest and jungle rubber in density of larger trees (DBH over 10 cm).

Terrestrial pteridophytes

Species-accumulation curves for all terrestrial pteridophyte species in our dataset and for the 'forest species' subset are shown in Fig. 7.

The 'all species' curves for terrestrial pteridophytes in Fig. 7 indicate that species richness was higher in jungle rubber than in both forest and rubber plantations, with forest having the lowest species richness. However, all differences were small in absolute terms, and Fig. 7 seems to show a flattening trend in the rubber plantations data at larger areas for which we did not have data from forest. The curves for 'forest species' show larger differences in species richness. Forest had the highest richness of 'forest species', followed by jungle rubber, and rubber plantations, which had the lowest richness of 'forest species'. For further details on the terrestrial pteridophyte data see Beukema and Van Noordwijk (2004).

Birds: species-accumulation curves

Figure 8 shows species-accumulation curves based on the dataset of Danielsen and Heegaard (1995, 2000) for all birds, and for the subset of 'forest interior birds' of habitat group 1.

In Fig. 8, the 'all species' curves for primary forest and jungle rubber are close together, with only slightly higher species richness values for forest. The 'forest species' curves on the other hand show higher species richness in forest than in jungle rubber with respect to bird species that generally prefer the forest interior. Rubber plantations had much lower bird diversity than primary forest and jungle rubber, both for 'all species' and for the 'forest species' subset.

Bird species richness found in the rapid survey by Jepson and Djarwadi (1999) in the three land use types was similar to that found by Danielsen and Heegaard (Fig. 8) when all species were included. At a sampling effort of 6 man-hours, Jepson and Djarwadi found 30, 33 and 20 species in forest, jungle rubber and rubber plantation respectively, where the average numbers of species in Fig. 8 at 6 man-hours were 31, 30 and 19, respectively. At a sampling effort of 12 man-hours, Jepson and Djarwadi found 42 species in forest, where in Fig. 8 the average number of species in forest was also 42. For 'forest species', the trends shown by the two datasets were the same: highest species richness in forest, lowest in rubber plantations, and intermediate values in jungle rubber. The actual numbers of 'forest species' found were not as similar: Jepson and Djarwadi found 19, 14 and 7 species in forest, jungle rubber and rubber plantation respectively at 6 man-hours, versus an average of 23, 16 and 2 species in Fig. 8. At 12 man-hours, Jepson and Djarwadi found 26 species in forest, versus an average of 32 species in Fig. 8. Bird data by Thiollay (1995) could not be related to sampling effort in man-hours, so we could not compare this data to our species-accumulation curves.

With regard to bird species composition in primary forest and jungle rubber, the data by Danielsen and Heegaard (appendix 2) show that about half of the species in both primary forest and jungle rubber were also found in the other land use type. A total of 35 species (of which 80% were 'forest species') were found uniquely in primary forest, 32 species (of which 63% were 'non-forest species') were found uniquely in jungle rubber, while 32 species (of which 72% were 'forest species') were found both in primary forest and in jungle rubber.

Birds: habitat preference

We used the grouping of bird species by preferred habitat to compare all three datasets with respect to relative importance (in terms of relative number of species) of the three habitat groups in the three land use types, see Fig. 9.

Results for the different datasets were close together for primary forest and for jungle rubber (maximum 15% difference between datasets), and followed the same, expected pattern of a decrease in 'forest birds' and an increase in birds of more open landscapes from forest to jungle rubber. The dataset of Danielsen and Heegaard showed a continuation of this trend in rubber plantation, as expected. The rubber plantation sample of Jepson and Djarwadi on the other hand contained relatively many 'forest birds' and relatively few birds of habitat group 2 (birds of edges/gaps/plantations).

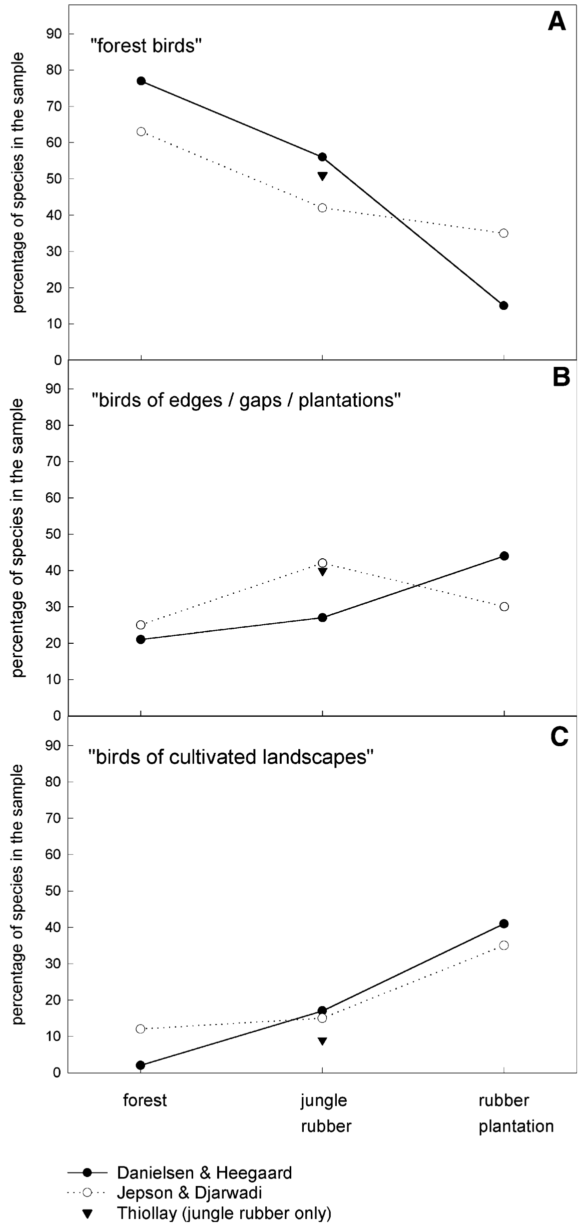

Fig. 9 Number of bird species belonging to habitat groups (roughly with habitat group 1 = forest birds, 2 = birds of edges/gaps/plantations, and 3 = birds of cultivated landscapes, see Methods section), as a percentage of the total number of bird species found in the land use type, for each dataset separately. Within each land use type, addition of percentages across graphs A, B & C will yield 100% for each dataset

Relative species richness in jungle rubber

In Fig. 10 we summarised results of Fig. 2, 4, 5, 7 and 8 by plotting species richness in jungle rubber as a percentage of species richness in primary forest, by area for plants and by sampling time for birds.

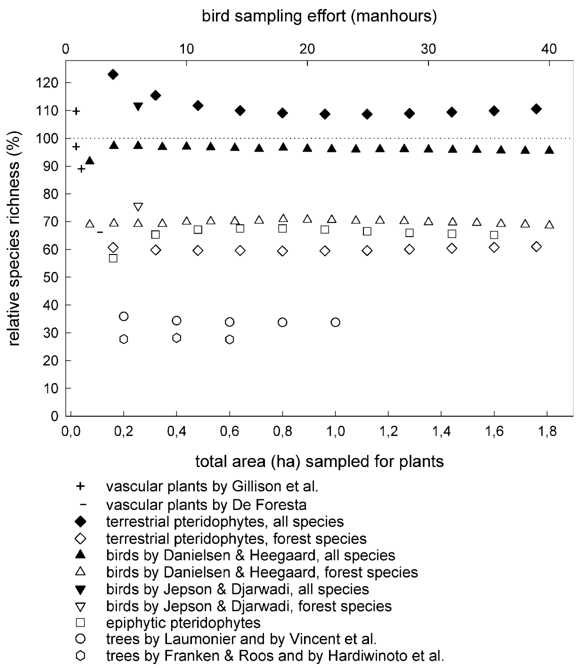

Fig. 10 Species richness in jungle rubber as a percentage of species richness in primary forest for all vascular plants, for terrestrial and epiphytic pteridophytes, for trees, and for birds. Scale for plants in hectares (lower axis), scale for birds in man-hours (upper axis). Data from Fig. 2, 4, 5, 7 & 8. The duplicates by Gillison et al. are displayed both separately (0.02 ha) and combined (0.04 ha). The percentage for De Foresta's dataset is based on the average of two transect lines in jungle rubber compared to one line in primary forest, and is placed at an estimated sampled area of 0.1 ha

Figure 10 shows that percentages found for relative species richness of terrestrial pteridophytes, birds and epiphytic pteridophytes in jungle rubber, as compared to primary forest, were far apart and that there was no similarity in species richness patterns for these groups. However if we consider the subset of 'forest species' of terrestrial pteridophytes and birds, and we take into account that epiphytic pteridophytes are largely 'forest species' by nature, we find for relative species richness of those 'forest species' in jungle rubber as compared to primary forest a common range of 60–70%. Relative species richness of trees was much lower, around 30%. A reliable percentage for vascular plants as a whole could not be established because available data were all in the range where scale effects are still influential.

In Fig. 10, scale effects appear only in the first few points of the pteridophyte and bird data series, followed by rather stable percentage values for relative species richness in jungle rubber as compared to primary forest. Note that from this graph we cannot derive the minimal sample size that would have been sufficient to arrive at a stable estimate of the relative species richness percentage, because for each point in Fig. 10 we used information from our full dataset, whereas smaller datasets would not necessarily show levelling off of the percentages at the same point as in our graph.

Discussion and conclusions

Sampling effects

Sample size and location

Sampling in one or two jungle rubber gardens only is not likely to give a result that is representative of the jungle rubber land use type as a whole, because of the mosaic character of jungle rubber and the occurrence of scale effects. Also the location(s) of the sample relative to other land uses may have a large influence on the results.

For vascular plants, Fig. 2 indicates a sampling scale effect similar to that found by Hamer and Hill (2000) for Lepidoptera. In the 0.02 ha plots, no negative effect of disturbance on species richness is found for conversion of forest to jungle rubber, whereas a trend of declining species richness seems to become apparent when species data from the duplicate plots are combined to show results for 0.04 ha. The larger sample by De Foresta shows an even stronger negative effect of disturbance on species richness of vascular plants.

The difference between the two datasets for vascular plants in results for the rubber plantations is most probably due to the choice of plot location. The rubber plantation sampled by Gillison et al. (1999) was owned by a private farmer (interviewed by H. Beukema) who stopped yearly fertiliser application 8 years before the sampling took place, and who used herbicides only once, 13 years before sampling. This rubber plantation plot was part of a relatively small section of rubber plantations in a largely forested area. De Foresta sampled a rubber plantation at Sembawa Research Centre (South Sumatra province) where fertilisers and herbicides were applied more intensively, and where the surroundings consisted mostly of cultivated lands.

Jepson and Djarwadi sampled the same rubber plantation as Gillison et al. for their bird study, and we suspect that the overrepresentation of 'forest birds' in their rubber plantation data (Fig. 9A) was an effect of the sampling location being close to forest. Keeping in mind that they sampled for a relatively short time in a single rubber plantation, the choice of location can have this large an effect on the results.

For birds, conclusions from our species-accumulation curves (Fig. 8) were not in agreement with the rarefaction curves of Thiollay (1995) for forest and jungle rubber. Thiollay found a much higher overall species richness in forest than in jungle rubber whereas we found almost no difference between our 'all species' curves for forest and jungle rubber. Thiollay (1995) mentioned a possible bias caused by differences in altitude and topography, and we suspect that indeed the forest samples were not really comparable to the jungle rubber samples in this case. The forest samples in Thiollay's study were a mixture of lowland and hill samples from three different locations as far as 685 km apart, whereas the jungle rubber samples were all from a single lowland location. The greater altitudinal and geographical range of the forest samples may have caused the higher species richness in forest as compared to jungle rubber. For this reason we did not include Thiollay's forest samples in our analyses.

Surrounding landscape matrix

Jungle rubber gardens are never far from a river, road or village, usually within a distance of about 5 km, as heavy slabs of coagulated rubber need to be carried out of the gardens towards a river or road for further transportation, and tapping is often daily. This has resulted in a landscape where adjacent gardens of different age and management intensity form broad bands along rivers and roads and around villages, and where jungle rubber areas belonging to different villages are often connected along rivers throughout the landscape. Historically, those jungle rubber areas were embedded in a matrix of lowland rainforest. Logging, forest fragmentation and conversion have since changed that matrix in large areas, especially in the lowlands of the central part of Jambi province. Most of our sampling in jungle rubber took place from 1991 to 1999, when major land use change was ongoing. Depending on the location where the sampling took place, the surrounding matrix either somewhat reflected the historical situation with the nearest forest being a large forest area, although sometimes already (partly) altered by logging, or the new situation in which the matrix had been drastically altered and the nearest forest was a small forest fragment or a somewhat larger area of fragmented and logged forest.

Land use change processes may have affected our results in different ways depending on the sampling location and the sampled group. The three studies on birds were all in areas where the nearest forest was a large forest area. Riau province, where Danielsen and Heegaard sampled, was in the 1990s still much less logged and deforested than Jambi province (pers. comm. F. Stolle). The primary forest in their sample was within an area of approximately 160,000 ha of primary forests, about 3 km away from the jungle rubber. The jungle rubber in their sample was adjacent to slash-and-burn areas and low secondary growth. Jepson and Djarwadi sampled in a jungle rubber garden in a largely agricultural area with rubber plantations and low secondary vegetation, at about 13 km from a large forest concession area in the north of Jambi province. Their primary forest sample was in a 900 ha primary forest study area within the concession. Thiollay sampled in jungle rubber gardens about 10 km away from the edge of the forested area of the foothills of the Barisan Range. Although the immediate plot surroundings in the bird studies consisted mostly of other jungle rubber gardens, plantations and agricultural land, the large forest areas nearby may have been a source for birds recorded in the jungle rubber. The results of the bird studies may not be as representative of jungle rubber gardens in more deforested areas, where bird species richness and composition may be somewhat different.

For plants, nearby forests can be important as source areas for both plant seeds and populations of pollinators and dispersers. The jungle rubber plots of both De Foresta and Gillison et al. were in areas where the nearest forest was a large forest area. De Foresta sampled near the Barisan Range, in the same area as the bird study by Thiollay. One of his jungle rubber transects was located in the middle of a relatively small agroforest area of a few ha, next to a 4–5 km belt of slash-and-burn mosaic with fallows less than 5 years old that bordered the forest. The other jungle rubber transect was in a large rubber agroforest area of hundreds of ha that was connected to the forest. The transect was located at about 1 km from the border of this forest. Gillison et al. sampled the same plots as Jepson and Djarwadi, described above. The results of the vascular plant studies by De Foresta and Gillison et al. may not be as representative of jungle rubber gardens in more deforested areas, where overall plant species richness and composition may be somewhat different.

For pteridophytes, the influence of the distance to forest and the size of forest fragments may be less important, as pteridophytes do not require pollinators, and spores are wind-dispersed. Results are likely to be representative for jungle rubber in Jambi, as pteridophytes were sampled in a wide range of locations both in the central part of Jambi province and in the more forested areas near the Bukit Tigapuluh range. Distance to primary forest ranged from 2 km to 37 km, and averaged 13 km.

The main datasets for trees in jungle rubber, by Vincent et al. and Hardiwinoto et al., were collected in a now largely deforested area in the central and southern part of Jambi province. Distance to small fragments of primary forest ranged from 2 km to 30 km, and averaged 17 km. Some plots may have been closer to a somewhat larger area of fragmented and logged forest than to the small primary forest fragments for which distances were calculated. While sampling locations represented a largely deforested landscape, the dataset probably reflects a past situation in which more forest was present in the area because only trees with a minimum size of 10 cm DBH were selected, creating a time lag.

The future potential of jungle rubber to contribute to the conservation of forest species will largely depend on the extent to which viable populations can be maintained inside jungle rubber areas, and on the availability of forest nearby as a source area for biodiversity in jungle rubber.

Sampling method

For tree data, the largest forest dataset consisted of 6 ha of contiguous subplots within one large forest plot, whereas jungle rubber datasets consisted mostly of plots from different gardens in different locations. Jungle rubber gardens are usually small, varying in size from less than a hectare to a few hectares. The largest jungle rubber dataset that consisted of contiguous subplots was 1 ha in size and was collected in one garden. Although comparable in method to the large forest dataset, this dataset from a single garden may not have represented tree diversity in the mosaic of the jungle rubber land use type as well as the larger (3.2 ha) dataset that was collected in many different gardens.

For birds, there may have been variations in detectability caused by differences in vegetation structure. Some jungle rubber gardens are more managed than others, and have a more open understorey. Some cryptic and understorey bird species may have been easier to detect in those gardens than in primary forest. Most birds were however detected by their vocalisations, so differences in detectability caused by habitat variations is unlikely to be important (see Danielsen and Heegaard 1995 p. 83 where this is further discussed).

Representativeness of groups

When species richness is compared over a range of land uses, different patterns emerge for different groups. In Costa Rica, Harvey et al. (2006) found that dung beetle species richness was greatest in forests, intermediate in cocoa agroforestry systems, and lowest in plantain monocultures, while mammal species richness was higher in forests than in either cocoa agroforestry systems or plantain monocultures. In a study in Cameroon, Lawton et al. (1998) assessed whether changes in species richness of different groups of organisms (birds, soil nematodes and several arthropod groups) over a disturbance gradient from near primary forest to fallow vegetation were correlated. They found that ''on average, only 10–11% of the variation in species richness of one group is predicted by the change in richness of another group'' and conclude that ''attempts to assess the impacts of tropical forest modification and clearance using changes in the species richness of one or a limited number of indicator taxa to predict changes in richness of other taxa may be highly misleading''. Our results for vascular plants and birds point in the same direction with regard to species richness. Terrestrial pteridophytes were found to be slightly more species rich in jungle rubber than in primary forest, whereas species richness of epiphytic pteridophytes and trees was much lower in jungle rubber than in primary forest. Species richness of vascular plants as a whole was lower in jungle rubber than in primary forest, but this could indeed not be predicted from the relative species richness of one or a limited number of subgroups. For birds we found no real difference in total species richness between jungle rubber and primary forest within the relatively short sampling time. We agree with Lawton et al. (1998) that changes in overall species richness of individual taxa or subgroups as such are not informative enough to study impacts of forest conversion. However, our findings suggest that when we take ecological characteristics of species into account, relative species richness of 'forest species' may be a useful indicator of the biodiversity conservation value of the jungle rubber land use type (see also Basset et al. 1998). As the biodiversity conservation value of jungle rubber tends to be overestimated by including species that are not usually associated with primary forest, we see a clear need for ecological information at the species level to allow for species classifications that are relevant to conservation.

Danielsen and Heegaard (2000) found a reduction of specialised insectivore birds of the mid-canopy and understorey, and of woodpeckers, in jungle rubber as compared to forest; they also found that birds are affected by regular presence of rubber tappers and by hunting, reflected in a reduction of pheasants. Several studies in tropical America and Africa concur with our results: high bird species richness in agroforests as compared to nearby forests, but altered composition with regard to ecological groups. For example, Tejeda-Cruz and Sutherland (2004) found that shade coffee plantations in southern Mexico had bird diversity levels similar to, or higher than, natural forest, but supported mostly generalist species, not forest specialists. Shade cacao plantations in Bahia (Faria et al. 2006) were characterized by a loss of understorey specialists and an increase of more open area and generalist bird species as compared to nearby forest fragments. In shade-grown yerba mate in Paraguay, 66% of the 145 bird species that were regularly recorded in nearby forest were also regularly recorded in the plantation, but forest floor and understorey bird species were absent (Cockle et al. 2005). In Cameroon, a number of bird groups and guilds were found to be significantly different in species richness in forest, agroforestry systems (cacao, coffee, plantain), and annual cultures (Waltert et al. 2005).

Conservation and production in rubber agroforests

The role that rubber agroforests can play in biodiversity conservation is limited by the fact that it is a production system that has to be profitable for the farmer. Management practices such as planting, weeding and selection as well as the length of the planting cycle affect vegetation composition and recolonisation by wild species. Even when rubber gardens are not regularly cleaned, farmers generally support desired tree species, either wild or planted, by protecting seedlings, while unwanted tree species are actively removed from gardens by slashing and ring-barking.

Werner (1999) compared the vegetation of secondary forest, cleaned rubber gardens and unmanaged rubber gardens in Kalimantan, and concluded that ''regular selective cleaning practices are the major reason for differences in botanical composition and biodiversity of rubber gardens and unmanaged fallow''. Rubber gardens in her study had lower numbers of tree species than unmanaged secondary forests. She also found that the difference in number of species between secondary forest and rubber gardens was more pronounced for tree species than for other vegetation groups. In Singapore, Turner et al. (1997) found that the mean tree species number per plot in a diverse type of approximately 100-year-old secondary forest was about 60% of that in primary forest, which is much higher than the relative tree species richness in jungle rubber found in this study (around 30%).

Length of the planting cycle is a major limitation for biodiversity conservation in jungle rubber. Jungle rubber is replanted when the number of rubber trees and latex production become too low to be profitable, on average after about 40 years. Late-successional trees may not reproduce in such a short time, and plant groups such as epiphytes that depend on later successional stages of forest may not have had enough time to establish and reproduce. We found that several epiphytic pteridophyte species observed in forest were never found in jungle rubber. Those species may be limited to much older secondary forest or to primary forest. Epiphytic orchids are known to colonise secondary forest more slowly than epiphytic pteridophytes (Johansson 1974). We observed that epiphytic orchids were present in fewer jungle rubber plots than epiphytic pteridophytes (Fig. 3), with lower abundance, and were never found flowering or with seeds in jungle rubber gardens.

Although birds can seek out older and less managed gardens, some habitat characteristics of primary forest are rare or lacking in disturbed forest, resulting in a changed community structure of birds with respect to feeding guilds (Danielsen 1997; McGowan and Gillman 1997).

While we acknowledge that irreparable damage has been done to lowland forests in Sumatra, and that many species are threatened and unlikely to find a suitable habitat in jungle rubber or other disturbed forest types (see also Waltert et al. 2004), we do want to emphasize the role that jungle rubber can play in the landscape. The importance of jungle rubber for biodiversity conservation in a largely deforested landscape, increasingly dominated by plantations, cannot be stressed enough. The very low richness values for 'forest species' of plants and birds in rubber plantations and the absence of whole groups of organisms from rubber plantations as shown in this paper are clear indicators of the impoverished landscape that is being created by the current large scale conversion process. Although biodiversity in jungle rubber is much reduced compared to primary forest, it is an invaluable biodiversity refuge especially in areas bordering (logged) forest.

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Appendix 1

Species of epiphytic pteridophytes found in 0.16 ha plots in primary forest ($N = 10$), jungle rubber ($N = 23$) and rubber plantations ($N = 17$) in the lowlands of Jambi Province, Sumatra; data by H. Beukema. Values reflect the percentage of plots in each land use type in which the species was found. Families are according to Kubitzki (1990).

Family	Species	Primary forest	Jungle rubber	Rubber plantation
Aspleniaceae	*Asplenium nidus L./Asplenium phyllitidis Don*	100	70	47
Aspleniaceae	*Asplenium pellucidum Lam.*	0	4	6
Davalliaceae	*Davallia angustata Wall. ex Hook. & Grev.*	10	0	0
Davalliaceae	*Davallia denticulata (Burm. f.) Mett. ex Kuhn var. denticulata*	50	43	12
Davalliaceae	*Davallia heterophylla J. Sm.*	20	0	0
Davalliaceae	*Davallia solida (Forst.) Sw. var. solida*	90	35	18
Davalliaceae	*Davallia triphylla Hook.*	50	17	0
Dryopteridaceae	*Pleocnemia irregularis (C. Presl) Holtt.*	0	4	0
Lycopodiaceae	*Lycopodium sp.*	10	0	0
Nephrolepidaceae	*Nephrolepis biserrata (Sw.) Schott*	10	30	18
Polypodiaceae	*Drynaria quercifolia (L.) J.Sm.*	50	17	24
Polypodiaceae	*Drynaria sparsisora (Desv.) Moore*	100	87	47
Polypodiaceae	*Goniophlebium percussum (Cavanilles) Wagner et Grether*	20	4	0
Polypodiaceae	*Lecanopteris crustacea Copel.*	20	0	0
Polypodiaceae	*Loxogramme avenia (Blume) Presl*	10	0	0
Polypodiaceae	*Loxogramme cf. scolopendrina (Bory) Presl*	10	0	0
Polypodiaceae	*Microsorum membranifolium (R. Br.) Ching*	0	0	6
Polypodiaceae	*Microsorum punctatum (L.) Copel.*	20	26	29
Polypodiaceae	*Microsorum scolopendria (Burm. f.) Copel.*	0	0	12
Polypodiaceae	*Platycerium coronarium (Koenig) Desv.*	10	0	12
Polypodiaceae	*Platycerium ridleyi Christ.*	20	0	0
Polypodiaceae	*Pyrrosia angustata (Sw.) Ching*	90	52	24
Polypodiaceae	*Pyrrosia lanceolata (L.) Farwell*	60	13	24
Polypodiaceae	*Pyrrosia longifolia (Burm.) Morton*	10	0	18
Polypodiaceae	*Pyrrosia piloselloides (L.) Price*	0	17	35
Polypodiaceae	*Selliguea lateritia (Baker) Hovenkamp*	10	0	0
Vittariaceae	*Antrophyum callifolium Bl.*	10	9	0
Vittariaceae	*Vittaria elongata Sw.*	90	65	6
Vittariaceae	*Vittaria ensiformis Sw.*	70	43	0
Vittariaceae	*Vittaria scolopendrina (Bory) Thwaites*	0	4	0
	Number of species	24	18	16

Appendix 2 List of birds with habitat preference classification, number of individuals in the datasets of Danielsen & Heegaard (D&H) and Thiollay (TH), and presence (1) or absence (0) in the dataset of Jepson & Djarwadi (J&D). Nomenclature follows Andrew (1992). Habitat class 1 = forest birds, 2 = birds of edges/gaps/plantations, and 3 = birds of cultivated landscapes; see Methods section).

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Abroscopus superciliaris	Yellow-bellied Warbler	2	0	0	0	7	0	0	0	0
Accipiter gularis	Japanese Sparrowhawk	3	0	0	0	0	0	0	0	1
Accipiter trivirgatus	Crested Goshawk	1	0	0	0	1	0	0	0	0
Aegithina tiphia	Common Iora	2	0	0	0	10	0	0	0	0
Aegithina viridissima	Green Iora	1	3	0	5	10	0	0	0	0
Aethopyga siparaja	Crimson Sunbird	2	0	1	0	6	0	0	0	0
Alcippe brunneicauda	Brown Fulvetta	1	0	0	0	10	0	0	0	0
Amaurornis phoenicurus	White-breasted Waterhen	3	0	0	6	0	0	0	0	0
Anorrhinus galeritus	Bushy-crested Hornbill	1	0	38	0	5	0	0	0	0
Anthracoceros albirostris	Asian Pied Hornbill	2	0	0	0	0	0	0	1	0
Anthracoceros malayanus	Black Hornbill	2	8	4	0	5	0	0	1	0
Anthreptes malacensis	Brown-throated Sunbird	3	0	0	0	21	1	0	1	0
Anthreptes rhodolaema	Red-throated Sunbird	2	0	0	0	8	0	0	0	0
Anthreptes simplex	Plain Sunbird	1	1	0	0	3	0	0	0	0
Anthreptes singalensis	Ruby-cheeked Sunbird	2	0	0	0	14	0	0	0	0
Aplonis panayensis	Asian Glossy Starling	3	0	0	0	0	1	1	0	0
Arachnothera affinis	Grey-breasted Spiderhunter	1	4	3	0	0	1	1	0	0
Arachnothera chrysogenys	Yellow-eared Spiderhunter	1	0	0	0	4	0	0	0	0
Arachnothera flavigaster	Spectacled Spiderhunter	1	0	0	0	6	0	0	0	0
Arachnothera longirostra	Little Spiderhunter	1	203	127	4	95	1	0	0	0
Arachnothera robusta	Long-billed Spiderhunter	1	0	0	0	1	0	0	0	0
Argusianus argus	Great Argus	1	59	0	0	0	0	0	0	0
Aviceda jerdoni	Jerdon’s Baza	1	1	0	0	0	0	0	0	0
Blythipicus rubiginosus	Maroon Woodpecker	1	1	0	0	0	0	0	0	0
Buceros rhinoceros	Rhinoceros Hornbill	1	3	0	0	4	1	0	1	0
Cacomantis merulinus	Plaintive Cuckoo	3	0	16	22	0	0	0	0	0
Cacomantis sonneratii	Banded Bay Cuckoo	2	0	0	0	1	1	0	1	0
Calorhamphus fuliginosus	Brown Barbet	2	0	4	0	38	0	0	1	0
Calyptomena viridis	Green Broadbill	1	17	0	0	0	0	0	0	0
Celeus brachyurus	Rufous Woodpecker	2	1	1	0	3	0	0	0	0
Centropus bengalensis	Lesser Coucal	3	0	15	0	1	0	0	1	1
Centropus sinensis	Greater Coucal	3	0	15	4	0	0	0	0	0
Cettia vulcania *	Sunda Bush-Warbler	1	0	0	0	0	0	0	1	0
Ceyx erithacus	Oriental Dwarf Kingfisher	1	0	0	0	0	1	1	0	0
Chalcophaps indica	Emerald Dove	1	5	4	0	0	0	0	1	1
Chloropsis cochinchinensis	Blue-winged Leafbird	2	0	0	0	33	0	0	0	0

Appendix 2 continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Chloropsis cyanopogon	Lesser Green Leafbird	2	0	0	4	4	0	0	0	0
Chloropsis sonnerati	Greater Green Leafbird	1	0	0	0	5	1	1	0	0
Chrysococcyx xanthorhynchus	Violet Cuckoo	2	0	0	0	6	0	0	0	0
Copsychus malabaricus	White-rumped Shama	1	17	14	1	28	0	1	0	0
Copsychus saularis	Oriental Magpie-robin	3	0	0	11	9	0	0	0	0
Coracina striata	Bar-bellied Cuckoo-shrike	1	0	0	0	0	1	0	0	0
Corvus enca	Slender-billed Crow	2	9	0	12	3	0	1	1	1
Corvus macrorhynchos	Large-billed Crow	3	0	8	0	0	0	0	0	0
Criniger bres	Grey-cheeked Bulbul	1	0	2	0	6	0	0	0	0
Criniger ochraceus	Ochraceous Bulbul	1	0	0	0	2	0	0	0	0
Criniger phaeocephalus	Yellow-bellied Bulbul	1	1	2	0	6	1	1	0	0
Culicicapa ceylonensis	Grey-headed Flycatcher	1	0	0	0	0	1	0	0	0
Cymbirhynchus macrorhynchos	Black-and-red Broadbill	2	0	0	0	1	0	0	0	0
Cyornis tickelliae *	Tickell's Blue Flycatcher	2	0	0	0	0	1	1	0	0
Cyornis turcosus	Malaysian Blue Flycatcher	1	0	4	0	1	0	0	0	0
Dicaeum cruentatum	Scarlet-backed Flowerpecker	2	0	2	0	20	0	0	0	0
Dicaeum trigonostigma	Orange-bellied Flowerpecker	2	0	0	0	56	1	1	1	0
Dicrurus aeneus	Bronzed Drongo	2	0	0	0	2	0	0	0	0
Dicrurus paradiseus	Greater Racket-tailed Drongo	2	81	37	6	14	1	1	1	0
Dinopium javanense	Common Goldenback	2	0	0	1	0	0	0	0	0
Dinopium rafflesii	Olive-backed Woodpecker	1	0	0	0	0	1	0	0	0
Dryocopus javensis	White-bellied Woodpecker	1	2	0	0	0	1	1	0	0
Ducula aenea	Green Imperial Pigeon	1	0	0	0	0	0	0	1	0
Eupetes macrocerus	Rail Babbler	1	2	0	0	0	0	1	0	0
Eurylaimus javanicus	Banded Broadbill	1	1	0	0	1	0	0	0	0
Eurylaimus ochromalus	Black-and-yellow Broadbill	2	58	0	8	5	0	0	1	1
Eurystomus orientalis	Common Dollarbird	2	0	0	0	1	0	0	0	0
Gallus gallus	Red Junglefowl	2	0	0	0	1	0	0	0	0
Gracula religiosa	Hill Myna	2	5	34	0	6	0	1	0	1
Halcyon chloris	Collared Kingfisher	3	0	3	0	0	0	0	0	0
Halcyon smyrnensis	White-throated Kingfisher	3	0	0	1	2	0	0	0	1
Harpactes diardii	Diard's Trogon	1	1	0	0	0	0	0	0	0
Harpactes duvaucelii	Scarlet-rumped Trogon	1	0	1	0	2	0	0	0	0
Harpactes kasumba	Red-naped Trogon	1	0	0	0	0	1	1	0	0
Harpactes orrhophaeus	Cinnamon-rumped Trogon	1	1	0	0	0	0	0	0	0
Hemicircus concretus	Grey-and-buff Woodpecker	2	0	2	0	15	0	0	0	0
Hemiprocne comata	Whiskered Tree-swift	2	0	0	0	0	0	1	0	0
Hemipus hirundinaceus	Black-winged Hemipus	2	0	0	11	19	0	1	0	0

Appendix 2 continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Hypogramma hypogrammicum	Purple-naped Sunbird	1	1	5	0	3	0	0	0	0
Hypothymis azurea	Black-naped Monarch	1	2	13	0	20	0	1	1	0
Hypsipetes charlottae	Buff-vented Bulbul	1	0	0	0	3	0	0	0	0
Hypsipetes criniger	Hairy-backed Bulbul	1	8	0	0	19	0	0	0	0
Irena puella	Asian Fairy Bluebird	1	1	3	0	10	0	1	0	0
Kenopia striata	Striped Wren-babbler	1	0	0	0	0	0	1	0	0
Lalage nigra	Pied Triller	3	0	0	2	0	0	0	0	0
Lanius cristatus	Brown Shrike	1	0	1	0	0	0	0	0	0
Lonchura leucogastra	White-bellied Munia	2	0	32	0	0	0	0	0	0
Lonchura striata	White-rumped Munia	3	0	7	296	0	0	0	0	0
Lophura erythrophthalma	Crestless Fireback	1	2	0	0	0	0	0	0	0
Loriculus galgulus	Blue-crowned Hanging-parrot	2	2	3	0	2	1	1	0	1
Macronous gularis	Striped Tit-babbler	2	47	22	12	8	0	0	1	0
Macronous ptilosus	Fluffy-backed Tit-babbler	1	4	38	0	8	0	0	0	0
Malacopteron affine	Sooty-capped Babbler	1	0	0	0	1	0	0	0	0
Malacopteron cinereum	Scaly-crowned Babbler	1	57	2	0	8	0	1	0	0
Malacopteron magnirostre	Moustached Babbler	1	4	0	0	28	1	1	0	0
Malacopteron magnum	Rufous-crowned Babbler	1	18	0	0	17	1	0	0	0
Megalaima australis	Blue-eared Barbet	2	6	0	0	39	0	0	1	0
Megalaima chrysopogon	Gold-whiskered Barbet	1	48	21	0	0	0	0	0	0
Megalaima haemacephala	Coppersmith Barbet	3	0	0	0	21	0	0	0	0
Megalaima henricii	Yellow-crowned Barbet	1	2	3	0	0	0	0	0	0
Megalaima mystacophanos	Red-throated Barbet	1	0	0	0	10	0	0	0	0
Megalaima rafflesii	Red-crowned Barbet	1	0	0	0	6	1	1	0	0
Meiglyptes tristis	Buff-rumped Woodpecker	2	0	1	8	0	0	0	0	0
Meiglyptes tukki	Buff-necked Woodpecker	1	0	5	0	2	1	0	0	0
Merops viridis	Blue-throated Bee-eater	3	0	0	0	0	0	1	1	1
Microhierax fringillarius	Black-thighed Falconet	2	0	0	0	1	0	0	0	0
Napothera macrodactyla	Large Wren-babbler	1	2	0	0	2	0	0	0	0
Nectarinia jugularis	Olive-backed Sunbird	3	0	0	0	0	0	0	0	1
Nectarinia sperata	Purple-throated Sunbird	2	0	0	0	7	0	0	0	0
Nyctyornis amictus	Red-bearded Bee-eater	1	0	1	0	12	0	0	0	0
Oriolus chinensis	Black-naped Oriole	3	0	1	2	0	0	0	0	0
Oriolus xanthonotus	Dark-throated Oriole	1	46	4	0	1	0	0	1	0
Orthotomus atrogularis	Dark-necked Tailorbird	3	0	0	0	41	0	1	1	1
Orthotomus ruficeps	Ashy Tailorbird	3	0	1	32	29	1	1	0	0
Orthotomus sericeus	Rufous-tailed Tailorbird	2	0	6	0	2	0	1	0	0
Pelargopsis capensis	Stork-billed Kingfisher	3	0	1	0	0	0	0	0	0

Appendix 2 continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Pellorneum capistratum	Black-capped Babbler	1	1	54	0	2	0	0	0	0
Pericrocotus cinnamomeus	Small Minivet	2	0	0	2	0	0	0	0	0
Pericrocotus flammeus	Scarlet Minivet	1	0	0	0	6	0	0	0	0
Philentoma pyrhopterum	Rufous-winged Philentoma	1	2	0	0	0	0	0	0	0
Philentoma velatum	Maroon-breasted Philentoma	1	8	0	0	0	0	0	0	0
Picus puniceus	Crimson-winged Yellownape	1	0	0	0	1	0	0	1	1
Platylophus galericulatus	Crested Jay	1	3	0	0	0	0	0	0	0
Platysmurus leucopterus	Black Magpie	1	0	0	0	3	0	0	1	1
Pomatorhinus montanus	Chestnut-backed Scimitar-Babbler	1	3	0	0	0	0	0	0	1
Prinia atrogularis *	Hill Prinia	2	0	0	0	2	0	0	0	0
Prinia familiaris	Bar-winged Prinia	3	0	0	1083	0	0	0	1	0
Prinia flaviventris	Yellow-bellied Prinia	3	0	0	0	10	0	0	0	1
Prionochilus maculatus	Yellow-breasted Flowerpecker	1	4	4	0	37	0	0	0	0
Prionochilus percussus	Crimson-breasted Flowerpecker	1	0	3	0	37	0	0	1	1
Psittacula longicauda	Long-tailed Parakeet	2	137	44	300	0	0	0	0	0
Psittinus cyanurus	Blue-rumped Parrot	1	13	2	0	0	1	1	0	1
Ptilinopus jambu	Jambu Fruit-dove	1	0	2	0	0	0	0	0	0
Pycnonotus atriceps	Black-headed Bulbul	2	0	12	0	56	0	0	1	1
Pycnonotus brunneus	Red-eyed Bulbul	1	1	3	0	21	0	0	1	1
Pycnonotus cyaniventris	Grey-bellied Bulbul	1	1	0	0	0	0	0	0	0
Pycnonotus erythropthalmos	Spectacled Bulbul	2	4	0	0	154	0	0	0	0
Pycnonotus eutilotus	Puff-backed Bulbul	1	0	0	0	8	0	0	0	0
Pycnonotus goiavier	Yellow-vented Bulbul	3	0	50	1013	0	0	0	0	0
Pycnonotus melanicterus	Black-crested Bulbul	2	0	11	0	51	0	0	1	1
Pycnonotus melanoleucos	Black-and-white Bulbul	1	8	0	0	0	0	0	0	0
Pycnonotus plumosus	Olive-winged Bulbul	3	1	3	0	14	0	0	0	0
Pycnonotus simplex	Cream-vented Bulbul	1	0	4	0	74	0	0	1	0
Reinwardtipicus validus	Orange-backed Woodpecker	1	1	0	0	2	0	0	0	0
Rhamphococcyx curvirostris	Chestnut-breasted Malkoha	2	0	0	0	5	0	0	0	0
Rhinomyias olivacea	Fulvous-chested Rhinomyias	1	0	0	0	5	0	0	0	0
Rhinomyias umbratilis	Grey-chested Rhinomyias	1	2	0	0	0	0	0	0	0
Rhinoplax vigil	Helmeted Hornbill	1	26	0	0	0	1	1	0	0
Rhinortha chlorophaea	Raffles's Malkoha	2	0	1	0	2	0	0	0	0
Rhopodytes diardi	Black-bellied Malkoha	2	0	0	0	1	0	0	0	0
Rhopodytes sumatranus	Chestnut-bellied Malkoha	1	0	0	3	0	0	0	1	0
Rhyticeros corrugatus	Wrinkled Hornbill	1	0	2	0	0	0	0	0	0
Rhyticeros undulatus	Wreathed Hornbill	1	0	4	0	0	0	0	0	0
Sasia abnormis	Rufous Piculet	2	1	4	1	2	0	0	1	0
Spilornis cheela	Crested Serpent-eagle	2	7	0	0	1	0	0	0	0

Appendix 2 continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Stachyris erythroptera	Chestnut-winged Babbler	1	42	53	0	14	0	0	1	0
Stachyris maculata	Chestnut-rumped Babbler	1	6	1	0	9	0	0	0	0
Stachyris nigricollis	Black-throated Babbler	1	18	7	0	4	0	0	0	0
Stachyris poliocephala	Grey-headed Babbler	1	2	2	0	12	0	0	0	0
Stachyris rufifrons	Rufous-fronted Babbler	1	0	0	0	4	0	0	0	0
Surniculus lugubris	Drongo Cuckoo	2	0	0	0	1	0	0	1	0
Terpsiphone paradisi	Asian Paradise-flycatcher	1	6	3	0	1	0	1	0	0
Treron olax	Little Green Pigeon	2	3	0	0	0	0	0	0	0
Treron vernans	Pink-necked Green Pigeon	2	0	0	8	5	0	1	0	0
Trichastoma abbotti	Abbott's Babbler	1	0	0	0	0	0	1	0	0
Trichastoma bicolor	Ferruginous Babbler	1	16	0	0	4	0	0	0	0
Trichastoma malaccense	Short-tailed Babbler	1	29	56	0	1	0	0	1	0
Trichastoma pyrrogenys	Temminck's Babbler	1	4	0	0	0	0	0	0	0
Trichastoma sepiarium	Horsfield's Babbler	1	0	0	0	0	1	1	0	0
Zanclostomus javanicus	Red-billed Malkoha	2	1	0	0	2	0	0	0	0

* Record should be considered preliminary until documentation is available

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